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# FURTHER NOTES ON THE PALEONTOLOGY OF ARRESTED EVOLUTION

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THE writer has in a former paper<sup>1</sup> endeavored to follow up the causes of persistence as seen from the side of the paleontologist. Using as a basis the genera which appear in Zittel-Eastman's Textbook of Paleontology (1913) and defining as persistent all genera which pass through more than two periods, the following data relative to number of persistent genera (*A*), total number of genera cited (*B*), and percentage of persistent genera (*C*) were obtained:

|                                           | <i>A</i> | <i>B</i> | <i>C</i>                  |
|-------------------------------------------|----------|----------|---------------------------|
| Foraminifera.....                         | 48       | 86       | 56                        |
| Sponges.....                              | 9        | 149      | 6                         |
| Corals.....                               | 46       | 237      | 15                        |
| Echinodermata:                            |          |          |                           |
| Crinoidea.....                            | 5        | 277      | 2                         |
| Cystoidea.....                            | 0        | 96       | 0                         |
| Blastoidea.....                           | 1        | 23       | 4                         |
| Ophiuroidea.....                          | 0        | 25       | 0                         |
| Asteroidea.....                           | 5        | 43       | 11                        |
| Echinoidea.....                           | 19       | 191      | 10                        |
| Bryozoa.....                              | 68       | 306      | 22                        |
| Brachiopoda.....                          | 33       | 384      | 9                         |
| Mollusca:                                 |          |          |                           |
| Pelecypoda.....                           | 78       | 446      | 16                        |
| Scaphopoda.....                           | 5        | 18       | 27                        |
| Gastropoda.....                           | 126      | 420      | 30                        |
| Pteropoda (so-called).....                | 5        | 17       | 29                        |
| Pulmonata.....                            | 7        | 65       | 11                        |
| Cephalopoda ( <i>a</i> ) Nautiloidea..... | 12       | 170      | 7                         |
| ( <i>b</i> ) Ammonoidea.....              | 0        | 455      | 0                         |
| ( <i>c</i> ) Dibranchiata.....            | 0        | ...      | 0                         |
| Crustacea                                 |          |          |                           |
| Trilobita.....                            | 6        | 131      | 4.5                       |
| Ostracoda.....                            | 18       | 68       | 26.5                      |
| Cirripedia.....                           | 4        | 20       | 20                        |
| Malacostraca.....                         | 7        | 134      | 4.5                       |
| Arachnida.....                            | 3        | 66       | 4.5                       |
| Selachii.....                             | 16       | 168      | 9.5 (in<br>first edition) |

<sup>1</sup> R. Ruedemann, "The Paleontology of Arrested Evolution." Presidential Address. Albany, 1916. New York State Museum Bull. 196, 1918, pp. 107-138.

Dipnoi, Teleostei, Reptilia each have one in the 1896 edition of Zittel-Eastman. The vertebrate volume had not yet appeared of the second edition.

From an analysis of the percentages we drew the following inferences:

1. The lower classes tend in general to have more persistent types than the higher.

2. Within each order and class, again, the lower subclasses tend to furnish the greater percentage of persistent forms.

3. Frequently the persistent genera form a primitive central stock from which numerous shorter lived genera branch off.

4. The stable conditions of the open ocean and deep sea (as in the Foraminifera) and the subterranean conditions favor persistence of types, the latter condition including the burying and boring forms.

5. Sessile forms contain more persistent types than the vagile benthos.

6. Persistent types prevail in much greater number among the marine forms than among the land and fresh-water animals. Among the continental forms again the limnal and fluviatile forms appear to be more persistent than the terrestrial forms.

7. Most persistent types are small and inconspicuous forms.

8. Many persistent genera show a slow development, a distinct climacteric period and a long post-climacteric period. Connected with this observation is the other that persistent genera which slowly develop never produce many species during a single geologic period.

9. Minor factors of persistence are seen in (a) extreme individual vitality (as in *Lingula* and *Crania*), (b) immense broods (as in *Ostrea* and *Limulus*), (c) extreme restriction in the matter of food, as in the eaters of carrion and refuse (*Capulidæ*, oyster, etc.).

The same criteria were found to hold, on the whole, in regard to the persistent species and the higher groups

(families and orders). In the latter case superior sets of offensive arms and defensive armors, early developed, appear to have helped to give stability to some, as in the scorpions (pincers and poison glands), limulids (leathery armor combined with burrowing habit and enormous broods). Some, as the turtles, have successfully specialized for protection.

In trying to reduce the multiplicity of factors to a few controlling agents, it was found "that these are the fixation of the 'over-taken' and post-climacteric types, the presence of stable physical conditions, and withdrawal in various ways from the fields where the struggle for existence is fiercest. The stable physical conditions have been found by many in the open ocean, by some in the deeper littoral regions of the oceans, by others again in subterranean fields, by some in the rivers and lakes of continental regions that remained undisturbed by folding. Withdrawal from the struggle for existence with other organisms has been accomplished by a variety of means, as by isolation, burrowing life, small, inconspicuous size, superior, often deadly, offensive and strong defensive arms, through restriction to poor fare, great power of endurance, etc."

In an analysis of the biologic factors that have permitted persistence, two entirely different groups of persistent types must be distinguished: (1) The post-climacteric types; (2) the primitive central stocks. The former rely on stable physical conditions and withdrawal from the arena of the struggle for existence, as far as possible; while the latter are frequently dominant in the very seats of war. We have termed the first *persistent terminals*, the others *persistent radicles*.

The persistent terminals were considered to have become so fixed in all their characters as to make them persistent partly by the factors of progressive fixation and partly by the fact that they have in various ways avoided the opposing factor of natural selection; their conservation thus being in fact due in part to their ge-

rontic condition and in part to the peacefulness of their surroundings.

The persistent radicles, on the other hand, were thought to owe their persistence to the fact that through their primitive nature they are still adapted to a greater variety of conditions and that while there may be considerable variation, it is around a still unspecialized, primitive form and thus difficult of recognition.

Or, expressing the same difference in terms of the four processes of heredity, ontogeny, environment and selection, around which, according to Osborn, the life and evolution of organisms continuously center, we found that "the difference between the two groups of persistent types, the relatively rigid terminals and the more variable radicles, consists in the fact that in the former all factors have become fixed and unresponsive to stimuli, only the selection still slowly acting, while the latter are so well adapted to a variety of conditions that no changes readily originate through any of the processes of environment, ontogeny and selection, which affect the whole stock, while at the same time no changes in the germ plasm are induced through hereditary tendencies."

The following notes are written with the intention partly to add certain new factors that appear to contribute to the persistence of forms, and that had not been taken into account in the first essay; and partly to enter deeper into the analysis of the ultimate causes of persistence made possible through more recent investigations into the nature of phylogenesis.

### 1. ADDITIONAL FACTORS OF PERSISTENCE

The new factors here mentioned have all to do with the methods of reproduction whose influence had not been recognized, in the first paper, in the percentage table of persistent genera.

(a) *Reproduction by Simple Division.*—In the Protozoa reproduction takes place by division without any

loss, so that there is no distinction between parent and offspring. There is no death and thus it is that Weismann and others have spoken of the "immortality of the Protozoa." It is certainly significant, in this connection, that among the Foraminifera 56 per cent. of the genera were found to be persistent and many were found to exhibit tremendous persistence, ranging from the Ordovician, Silurian, Carboniferous and Triassic to recent times, and that even species (see Ruedemann, *op. cit.* p. 126) are known to extend from Silurian, Devonian, Carboniferous and Triassic times to the present. These forms the writer designated as actual "immortal types" in contrast to the theoretically immortal protozoans of Weismann.

There occurs, however, among the protozoans besides this asexual mode of reproduction a group of processes that are clearly the primitive beginnings of fertilization. In these forms of conjugation different stages may be distinguished, viz., the mere congregation of cells in groups without visible exchange of plasms (cytotropy); the exchange of substance taking place only through osmotic processes; further conjugation, where real fusion of plasmas occurs but the cell-nuclei remain separate (plasmogamy); and finally such modes of conjugation, where also nuclear fusion of the conjugating cells takes place (karyogamy); and here again, the pairing cells may be either similar in size (isogamy), or even markedly dissimilar in size (anisogamy).

It is, however, to be remembered that the usual reproductive process among protozoans is simple fusion of ordinary vegetative cells and conjugation as a rule occurs at rare intervals in most forms, often only when unfavorable conditions arise, or as Maupas' experiments indicate, the individuals in the course of numerous successive asexual generations grow old.

(b) *Reproduction by Budding*.—This mode of asexual reproduction differs from that of division originally in the protozoans merely in the different sizes of the daughter-

cells and the mother-cell, but develops into a complex process in the multicellular forms. Distinct budding occurs already in the protozoans as in *Arcella*, where a number of small buds are constricted off all round. In sponges it is developed to such a degree that no one can fail to recognize the impossibility of drawing any rigid line between growth and asexual reproduction.<sup>2</sup> In the coelenterates asexual reproduction runs riot, as Geddes and Thompson state. It is, further, by far the prevailing mode of reproduction among the stock-building bryozoans; it also is common among marine worms, as with the famous palolo-worm off the coast of Samoa, and finally it is also frequently found among the tunicates.

The primitive character of this mode of reproduction can not be doubted. It probably in all cases is an inherited character that persisted from the ancestral protozoans. It has by many zoologists been considered as an acquired character among the tunicates, but Van Name<sup>3</sup> has lately advanced good reasons for the conclusion that it is also a primitive character among the ascidians inherited from their remotest ancestors and that it is not a faculty that can be acquired secondarily.

Budding leads to the formation of colonies or stocks. These as a rule are not favorable to a swimming or vagrant mode of life, hence by far the majority of budding forms are sessile, although there are a considerable number of exceptions in the swimming siphonophores, ctenophores, floating graptolites, and compound swimming worms and ascidians. Since most of the colonial stocks are sessile, budding has often been considered as having been induced by a sessile mode of life and thus held to be a function that could be acquired. Its absence among the sessile cirripedes seems, however, to support Van

<sup>2</sup> Geddes, Patrick, and Thompson, J. Arthur, "The Evolution of Sex," London and New York, 1914, p. 205.

<sup>3</sup> Van Name, Willard G., "Budding in Compound Ascidians and other Invertebrates, and its bearing on the Question of the Early Ancestry of the Vertebrates," *Bull. Amer. Mus. Nat. Hist.*, Vol. 44, art. 15, 1921, pp. 275-282.

Name's contention that this function can not be acquired when once lost.

The fact that the sessile forms contain more persistent types (corals have 15 per cent., bryozoans 22 per cent.) than the vagile benthos would suggest that budding may be a mode of asexual reproduction favorable to the persistence of types; and that it may be the cause of the large percentage of persistent types among the sessile forms. It must here, however, be considered that also the sessile Cirripedia which lack the function of budding, have furnished 20 per cent. of persistent types; and further that in all the classes here considered budding is associated with sexual reproduction, often, as in many coelenterates, in a regular alternation of generations. Moreover, the sexually reproducing brachiopods, gastropods and pelecypods have furnished large percentages of persistent types, a large number of which are sessile forms.

While thus budding would not seem to be the controlling factor in the persistence of the sessile forms, it is, nevertheless, true that budding may have a distinctly retarding effect upon the evolution of such forms, principally by the material decrease of the cases of sexual reproduction. As in the case of the corals, the number of new stocks that originate from sexual reproduction and finding a new lodging place, start new colonies, is very small when compared with the number of asexually produced individuals on the stocks. There are therefore many more generations of asexually than sexually produced individuals.

(c) *Reproduction by Hermaphrodites*.—Another factor that possibly may have contributed to the persistence of forms is hermaphroditism. Claus has pointed out that hermaphroditism finds most abundant expression in sluggish and fixed animals. "Among sponges, sea-anemones, corals, Polyzoa, bivalves, etc., we find frequent illustration of the association of fixedness and hermaphroditism" (Geddes and Thompson, *op. cit.*, p. 83). The origin of

hermaphroditism is still a matter of dispute (see Geddes and Thompson, pp. 83, 84) for while some, as Simon, attribute it to a plethora of nutrition (as especially in parasites), others are "content to interpret it as an adaptation to ensure fertilization, for the possibilities of pairing between separate sexes are certainly lessened if the animals are sluggish, sedentary or parasitic." There is likewise difference of opinion as to whether the stage of hermaphroditism is the lower, and the condition of distinct sexes has been derived from it (Gegenbaur), or whether it is a secondary condition, derived from primitive uni-sexuality as claimed by Pelseneer who considers it grafted on the female sex in Mollusca, Crustacea and Pisces (Geddes and Thompson, p. 84).

Considering its prevalence among the lowest classes with sexual reproduction, notably the sponges and corals, and again among the Cirripedia, we believe that hermaphroditism is in the former an inherited primitive character and in the latter an acquired one. At any rate, since it is so frequently and distinctly associated with sessility, as in the just mentioned Cirripedia, and in many pelecypods (oyster) and with sluggishness in other pelecypods and many gastropods, and since it is exactly these same groups which contain numerous persistent types, it seems probable that hermaphroditism is a further reproductive condition contributory to persistence.

(d) *Reproduction by Parthenogenesis*.—Parthenogenesis is the mode of propagation in at least one typically persistent genus, viz., *Apus*; but it has also become a confirmed physiological habit in other archaic types of crustaceans among the branchiopods, as notably in *Artemia*, the brine-shrimp, in *Branchipus*, and in *Limnadia*; further in the equally primitive water-fleas (*Daphnia* and *Moina*) and finally, among the ancient ostracods, also in some species of the common *Cypris*.

Of the whole class of Branchiopoda, which through paleontology, and notably through the recent amazing

discoveries of Walcott<sup>4</sup> in the Middle Cambrian of British Columbia, are proven to reach back to the oldest fossiliferous beds (in *Protocaris marshi* Walcott to the Lower Cambrian), *Apus* is the most remarkable and most often cited form in paleontologic literature. The writer has in a paper, now in press, shown that true *Apus*, identical in form of carapace and "shell glands" has been found in Permian beds of Oklahoma. It was before known from the Triassic Buntsandstein of the Vogesian Mountains. Its more than 70 pairs of gill-bearing feet and other primitive characters have made it the model of comparison for Paleozoic crustaceans, especially the trilobites. The Lower Cambrian *Protocaris marshi* is so closely allied to *Apus* that it was termed *Apus marshi* by Bernard. There is hence no doubt of the immense age of this type.

*Apus* is now so parthenogenetical in its reproduction that the males were not discovered until a hundred years after the description of the first and best known species (*A. cancriformis* Schäffer); and "von Siebold repeatedly investigated every member of a colony of *Apus*, once over 5,000 in number, without finding a single male. At other times he found one per cent. while in certain unknown conditions (probably when food is scarce and life generally unfavorable) the males may be developed in crowds" (Geddes and Thompson, p. 189). Similar conditions prevail in the brine-shrimp and the other branchiopods, cited above, as shown by Lereboullet and Nowikoff.

Parthenogenesis is associated with other strange habits in the three branchiopods, *Apus cancriformis*, *Limnadia hermanni*, and *Branchipus stagnalis*, which occur together in Europe. These creatures occur only after very wet seasons in puddles, road-ditches and other small pools, where their eggs have lain for decades in the dry mud, exposed to heat and frost. They develop with amazing

<sup>4</sup> Walcott, Charles D., "Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata," Smithsonian Miscellaneous Collections, Vol. 57, No. 6, 1912.

rapidity, *Apus cancriformis* reaching in two weeks a full size up to five inches,<sup>5</sup> produce an enormous number of eggs and die.

The origin of parthenogenesis in these forms as well as in the rotifers and certain insects has been fully discussed by Geddes and Thompson, and they are certain that it has originated as a degeneration from the ordinary sexual process (*ibid*, p. 198) and is no direct persistence of a primitive ideal state. Their theory of parthenogenesis is that the ova that develop parthenogenetically "are to be regarded as incompletely differentiated female cells, which retain a measure of katabolic (relatively male) products, and thus do not need fertilization" (they form only one polar body). "Such a successful balance between anabolism and katabolism is indeed the ideal of all organic life. In parasitic fungi, sexual reproduction disappears, and surrounding waste products presumably help the purpose otherwise effected by sexual organs, so peculiarities in the conditions of parthenogenetic ova may explain the retention of the normal balance which makes division possible without the usual stimulus of fertilization. Abundant and at the same time stimulating nutrition (Rolph), early differentiation of the sex-cells (Simon), the general preponderance of reproductive over vegetative constitution (Hensen), their liberation before the anabolic bias has carried them too far, are among these favoring conditions."

Parthenogenesis thus appears as a degenerative asexual process arising from peculiar conditions, the most important of which appears to be temporary over-nutrition. As in the other asexual modes of propagation, in division and budding, the inference suggests itself readily that this suppression of fertilization must induce persistence, for as Geddes and Thompson point out (*ibid.*, p. 193) the establishment of parthenogenesis and the ab-

<sup>5</sup> See Bruno Weigand, "Mitteilung über das Auftreten der Limnadia Hermannii Ad. Brgt. bei Strassburg im September 1912," *Mitt. der Philomat. Gesellsch. in Elsass-Lothringen*, Bd. 4, Heft. 5, Jahrgang 1912; 1913, p. 730.

sence of fertilization probably involves some diminution in the frequency and range of variability and thus the establishment of parthenogenesis will be a handicap to evolution.

In the case of *Apus*, and its other associated branchiopods as well, it is probable that the successful adaptation to special conditions is a strong contributing factor in the establishment of persistence, as pointed out by the writer in the former paper. It is possible that *Apus* has existed under these conditions from very early times.

Summing up the evidence on persistence of types from the habits of reproduction, it seems that simple division, budding, hermaphroditism and parthenogenesis have each contributed to this persistence and in their way acted as factors that arrested evolution, and that thus help to explain the relatively large percentage of persistent types in the protozoans, sponges, corals, molluscs and the just mentioned branchiopods among the crustaceans.

While the facts thus seem to indicate that these modes of reproduction, other than the normal process of fertilization, were favorable to persistence in fossil types, it is, in the present stage of our knowledge of the meaning of fertilization, not so simple to recognize the underlying cause of their arresting influence on evolution.

The simplest explanation would obviously be to see in fertilization the principal cause of *variation*, as such authors as Treviranus, Brooks, Galton, Weismann and Oscar Hertwig have done. Weismann has insisted that the intermingling of two "germ-plasms" is an important fountain of congenital variation. It can be readily seen that, under this view, the retarding effect of fission, budding and parthenogenesis consists in the exclusion, or restriction to long intervals, of fertilization, thereby reducing variability and the possible action of selection. It is also plausible under this view that mutual fertilization between hermaphroditic individuals tends toward equalization of characters; and this tendency towards equalization is still more increased by fertilization within

the same colonial stock or neighboring colonial stocks of plantations. The most important of the disadvantages resulting from hermaphroditism would then be to reduce the variability which is necessary to progress in the struggle for existence.

While, however, the possibility is not denied that fertilization may be a controlling factor in variation, as stated, *e.g.*, by William E. Kellicott in his "Text-book of General Embryology," 1913, p. 216, it is also obvious, according to the same author, that the evidence for this view is still scanty and uncertain and, moreover, there are two exactly opposed views as to the nature of the relation. While Hertwig maintains that the effect of fertilization is to limit variation within a species, Weismann asserts that the effect of syngamy or "amphimixis" is to cause or promote variation.

Kellicott (*op. cit.*, p. 214) states:

There is little direct factual evidence for or against these views, either one of which can be maintained upon theoretical grounds. In a few cases it is known that the amount of variability is not significantly different among sexually (gametically) or asexually (parthenogenetically) produced individuals of the same species. And from the standpoint of more recent studies upon heredity and variation the evidence is chiefly either negative or opposed to the idea that this relation constitutes an important element in the origin or present function of fertilization. The present aspects of this relation between fertilization and variation merge in the larger question of the relations with heredity.

While among the higher classes fertilization has become a stimulus to reproduction and a means of heredity, evidence from the lower groups tends to show that fertilization in its results has undergone evolution like every other organic function.

The view is widely accepted today (see Kellicott, p. 209) that among the Protozoa the processes of reproduction and fertilization are not fundamentally related, and the primary significance of fertilization must be sought in some other direction.

The observations made on protozoans have led to the

rejuvenation hypothesis, chiefly represented by Bütschli, Maupas and Richard Hertwig. "It has been found that protoplasmic activity tends gradually to diminish in intensity, and that associated with this diminution are certain morphological alterations in the structure and composition of the cell" (Kellicott, p. 209). These modifications are known as senescence, the senescent condition of the cell consisting frequently in the relatively large proportion of cytoplasm as compared with nuclear substance. Conjugation is assumed to restore the senescent protoplasm to its original condition of vigor, bringing about rejuvenation. It follows from this that protoplasmic activity is cyclic and that periods of senescence would lead to death unless fertilization should occur.

The real evidence for this cyclic character of the life processes of the Protozoans has been furnished by the observations of Maupas and Calkins on *Paramecium*. But observations of Jennings have shown that in different forms of *Paramecium* conjugation and rejuvenation may occur at very different intervals, and Woodruff has been able to prevent cyclic relations by substituting normal conditions for the artificial and more uniform ones of the laboratory. "By continually altering the character of the food, and by imitating in other ways the naturally variable conditions of pond life, he has been able to continue a single race of *Paramecium* for over five years" (quoting from Kellicott), during which period more than 3,000 generations were formed by simple fission. It follows from these observations that protoplasmic activity among the Ciliata may not be cyclic in character under certain conditions, and that when cyclic periods of depression or senescence do occur, the protoplasm may be restored to a condition of normal vigor, either by physical or chemical stimuli, or by fertilization (Kellicott, p. 212).

Fertilization is in these cases a form of reaction that takes place when external conditions become too uniform to bring forth the normal vegetative activities, and that

leads to an internal disturbance, thereby correcting the conditions of uniformity.

Applying these conclusions to our case of the persistent types it could be conceived that the reduction of fertilization to rare intervals, or its entire suppression, in the numerous persistent types that reproduce by fission, budding, parthenogenesis or hermaphroditism, produces a perpetual senescent condition that while not leading to death as in the rapidly dividing and sensitive *Paramecium*, finds its expression in the rigidity of the forms, recognizable in their lack of response to external stimuli and of further evolution, *i.e.*, in their persistence. Or in other words, infrequency or entire lack of rejuvenation through fertilization favors the persistent condition, at least among those persistent terminals that do not live under stable physical conditions. Those living under stable conditions may require fertilization as a necessary rejuvenating process counteracting progressive senescence and final extinction through lack of external stimuli. It would then appear that these lower modes of reproduction and very stable external conditions could not very well exist together.

However, as pointed out by Kellicott, there has been an evolution both of the process and of the consequences of fertilization, and the various possibilities as to the significance of fertilization are not mutually exclusive. It is therefore possible that the large percentage of persistent types among forms with more or less suppressed fertilization finds its explanation in some cases in the resulting lack of variation, in others in the resulting senescent and rigid condition of the race, and in still others it may be sought in the process of heredity, connected with fertilization. This last possibility will be dealt with in the following chapter.

#### REDUCTION OF FACTORS TO FUNDAMENTAL CAUSES

The investigation of the various groups of persistent types has indicated that there are a variety of factors

involved in their production. Many of these were found to be connected with the environment, others, acting through variability, or its lack, with selection, and still others with the processes of heredity and ontogeny. While of these four fundamental processes of evolution, viz., heredity, ontogeny, environment and selection, that of selection may account for the cases of persistence where variability has been reduced to a minimum, possibly by the lower modes of propagation mentioned above, and that of environment accounts for persistence in those cases where the environment has become so stable as to lack the actual stimulus for further development, it is obvious that still more important factors are involved in heredity and ontogeny that make for persistence in organisms, especially as it is seen in the post-climacteric forms, or persistent terminals. Both the conservative process of heredity and the much less rigid one of ontogeny appear to become more or less fixed and inaccessible to changes in persistent types.

None of these four processes gives any clue to the actual mechanics of the factors that induce persistence. In trying to trace the latter to its ultimate causes, it becomes, therefore, necessary to go beyond these processes, and to appeal to the important conclusions that have been obtained by modern experimentation and observation regarding the methods of inheritance and production of new characters by means of the genes or character-determiners of the heredity-chromatin.

Among these conclusions especially suggestive in regard to our problem, are the views advanced by Dürken and Salfeld.<sup>6</sup> These authors have, one through an analysis of all recent zoological experiments on evolutionary problems, the other through a corresponding analysis of the evolution among the fossil ammonites, arrived at the view that variability or the appearance of new characters, and of new combinations of characters is produced in differ-

<sup>6</sup> Dürken, B., and Salfeld, H., "Die Phylogenese. Fragestellungen zu ihrer exakten Erforschung," Berlin, Gebr. Bornträger. 1921.

ent ways, by the genes; and not only through internal factors, as claimed by the Neo-Darwinian school, but also through external ones as demanded by the Neo-Lamarckians. The genes, which are not only actual units, or representatives of definite phenotypic characters, but definitely delimited, material bodies, may not only produce new characters or character-combinations by a correlative and a combinative mode of ontogenetic evolution, or by loss of genes, as demonstrated by abundant experiments, but undoubtedly there takes place also a new formation of genes in evolution. This they hold to come about in successive stages through long enduring external influence, which first acts upon the cytoplasm of the cells and especially of the germ-cells. This cytoplasm in itself has been proven to have certain hereditary possibilities (plasmogenous heredity). Under long persistent external influence there form first preliminary stages of genes in the cytoplasm which finally, when a certain "threshold" (Schwelle) of continued strain is passed, become true genes of the heredity-chromatin. When this takes place, mutations appear abruptly (salto-mutations).

This view, here altogether too briefly presented, would explain the absence of evolution through salto-mutations in cases of persistence under continued stable exterior conditions, and since the cytoplasm is known also to influence directly the heredity-chromatin, also the absence of flueto-mutations or variations under stable conditions through lack of external stimulation.

However, in the cases where no new genes are formed by external influences, new characters could still appear through loss of genes or correlative or combinative modes of production of new genes from the old ones within the germ-plasm. This, however, leads to a restrictive cone of divergence ("Streuung") of the characters and through "self-differentiation" by a combinative mode of gene-production to the excessive characters of many terminal series (*e.g.*, dinosaurs); and to the rigid

persistent terminal types, on the other hand, through the gerontic rigidity of the remaining stock of genes. The principal causes of the persistence of terminal forms would then be the failure of production of new genes arising from the cytoplasm, through external influences, and the senescent rigidity of the remaining genes.

The persistent radicles, on the other hand, correspond to the extreme development of what Salfeld terms "*Konservativreihen*." There are series in which the salto-mutations appear in very long intervals, while the numerous side-branches (which furnish the index-fossils) develop by rapid salto-mutations. These persistent radicles are therefore able to undergo new periods of explosive and climacteric development ("*Virenz-perioden*" of Wedekind) and are thus still less absolutely persistent than the persistent terminals. In these conservative series, according to Salfeld, flucto-mutation is so prevalent that sharply defined "*species*," or better mutants, can not be separated, as notably in the phyla of *Phylloceras* and *Lytoceras* which range, qualitatively unchanged in their characters, through Jurassic and Cretaceous time. They thus represent true persistent radicles. This fact, combined with the observation of the vitality, relative primitive simplicity and adaptation to a variety of conditions of persistent radicles, pointed out by the writer in his former paper, suggests that the complex of genes is able to remain relatively undisturbed through external influences (only flucto-mutations appearing) in one part of these groups which persist as radicles, while those parts which become changed through the addition of genes by way of the cytoplasm turn into the side-branches by salto-mutation.